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A Revision of the Genus Copernicia

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A REVISION OF THE GENUS COPERNICIA

1. South American Species

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HISTORY

Species of *Copernicia* were originally included under *Corypha* L. by Arruda da Camara (1810), Humboldt, Bonpland, and Kunth (1816), and Martius (1824). Most of the species of *Corypha* have since been transferred to other genera, and now the name is used for species of Old World distribution. In 1838, Martius erected the genus *Copernicia*, describing one new species, *C. hospita*, and transferring two others, *C. cerifera* and *C. tectorum*, from *Corypha*. On page 319 of the same publication, he also transferred three other taxa from *Corypha* to *Copernicia;* these, however, have since been placed in other genera. *Copernicia nana* (H.B.K.) Mart. and *C. Pumos* (H.B.K.) Mart. are the sources for the erroneous reports of *Copernicia* from Mexico. Endlicher (1837), Kunth (1841), Martius (1844), Walpers (1849–52), Mueller (1858), Grisebach (1864, 1879), Drude (1882, 1889), and Bentham and Hooker (1883) treated *Copernicia* in various ways, but none added appreciably to the understanding of the genus or described any new species.

During his exploration of Cuba in the 1850's, Charles Wright collected two undescribed species of *Copernicia*. *Copernicia glabrescens* and *C. macroglossa*, based on Wright's collections, were first mentioned by Wendland as names only in Sauvalle (1873). Later, Beccari (1907) published these legitimately by attaching descriptions to them. In 1867, Macedo felt that Arruda da Camara's name should be commemorated with the carnauba palm; hence, he changed the name of this plant to *Arrudaria cerifera*.

Morong, in 1893, described two new species from Paraguay, *C. alba* and *C. rubra;* and Baillon (1895) and Barbosa Rodrigues (1898, 1903) gave brief accounts of the genus in their articles. In his treatment of the

1. Junior author (at left) and senior author in palm room at Chicago Natural History Museum, with numerous specimens of *Copernicia* collected in Cuba by the senior author during a period of about 15 years.

American Corypheae, Beccari (1907) recognized nine species of *Copernicia*, of which four were described as new. At the same time, he divided up the genus into the subgenera *Eucopernicia* and *Coperniciopsis*. Several years later, in his paper on the Cuban palms (1913), he listed four species of *Copernicia* from that island.

In the early 1900's, N. L. Britton, P. Wilson, J. F. Cowell, J. A. Shafer, and others, made a number of collecting trips to Cuba for the New York Botanical Garden. As a result of these trips, two new species of *Copernicia*, *C. Cowellii* and *C. rigida*, were described from the island by Britton and Wilson (1914). Between 1914 and 1925, H. Ekman collected thousands of plants in Cuba and Hispaniola for the Naturhistoriska Riksmuseum in Stockholm. The palms were sent to M. Burret of the Berlin-Dahlem Herbarium for determination. Subsequently, Burret (1929) published descriptions of six new species of *Copernicia*, including one named by Ekman himself, *C. gigas*. Burret (1928) also described another new species from Paraguay, *C. ramulosa*.

In his book on the Corypheae, published eleven years after his death, Beccari (1931) included essentially the same species of *Copernicia* as were in his 1907 work, but added illustrations.

The greatest addition to the list of names in *Copernicia* was made by León (1931, 1936) who, along with J. Roig, M. Curbelo, and J. Acuña, made extensive collecting trips throughout Cuba during the late 1920's and 1930's. In two articles, León described twenty-six taxa of *Copernicia* as new. Some of these were later considered synonymous by León himself and by the present authors. In a later treatment of the Cuban palms, León (1946) listed essentially the same taxa as in his earlier works.

Perhaps the largest and most diversified assemblage of *Copernicia* material was collected by the senior author of this paper during his numerous field trips to Cuba between 1942 and 1957. This material, plus hundreds of specimens borrowed from various herbaria, formed the basis for this revisional study of the genus. Recent publications by Dahlgren and Glassman (1958, 1959) have added two new taxa of *Copernicia* (*C. Leoniana* and *C.* × *Shaferi*) to the Cuban flora. In 1953, K. Markley, E. S. McLoud, and E. D. Kitzke, of S. C. Johnson & Son, Inc., made extensive collections of *Copernicia* specimens in various parts of Paraguay. These collections were most significant in our determining the existence of only one native species of *Copernicia* in central South America—namely, *C. alba* Morong.

MORPHOLOGY

Copernicia belongs to the subfamily Coryphoideae, which is characterized by having palmate leaves, nonscaly and mostly nondrupaceous

fruits, and seeds with a well-defined hilum. According to Burret's (1953) keys to the subfamilies of palms, the Coryphoideae are distinguished from the Lepidocaryoideae by the nonscaly rather than scaly fruits; from the Borassoideae by the nondrupaceous rather than drupaceous fruits and by the well-defined rather than obscure hilum; and from the Cocoideae, Nypoideae, Phoenicoideae, and Arecoideae by the palmate rather than pinnate leaves.

In the same article, Burret differentiates *Copernicia* from other genera of the Coryphoideae as follows: from *Schippia*, *Hemithrinax*, *Thrinax*, and *Coccothrinax* by its three-carpellate rather than one-carpellate ovary; from *Corypha*, *Sabal*, *Nannorhops*, and *Pritchardiopsis* by its partially united rather than completely united carpels; from *Trithrinax*, *Crysophila*, *Rhapis*, *Trachycarpus*, *Rhapidophyllum*, and *Chamaerops* by its partially united rather than completely distinct carpels; and from *Pritchardia*, *Washingtonia*, *Paurotis*, *Brahea*, and *Serenoa* by its deeply ruminate rather than nonruminate endosperm.

Size: Fully grown trees range in height from about one meter in *C. Cowellii* up to thirty meters in *C. alba*. Diameter at the widest portion of mature trunks varies from 12 cm. in *C. Brittonorum* to approximately 66 cm. in *C. Baileyana*.

Stem: The stems are erect, unbranched, and usually about the same diameter throughout, but are sometimes fusiform, as in *C. Baileyana*. The trunks are usually single, but occasionally in *C. Curtissii* there are several in a cluster. Leaf-scars are either prominent or obscure. Depending on age, the trunks are either smooth or covered partially or wholly with persistent petiole-bases. In some species the petiole-bases remain on the tree much longer than in other species.

Leaves: The leaves are borne at the apex of the stem in a dense crown. Blades are fan-shaped, and orbicular or cuneiform. They vary in length from about 60 cm. in *C. Cowellii* to about 180 cm. in *C. fallaense*. One blade of *C. rigida* which we have seen measures 202 cm. in length although normally the leaves of this species are considerably smaller. Blade-segments are variable in number on the same tree, but with a definite range in number within each species. Segments are elongate, plicate, finely parallel-veined, acuminate, and fused together from the base of the blade for two-thirds to three-fourths of their length. Short spines may be present near the base of the blades, on the surface or the margins, as in *C. macroglossa* and *C. rigida*. The blade-surface may be free of wax or may have wax deposits of variable density; in the latter case, usually both surfaces are waxy, but in *C. Cowellii* only the lower surface has wax. Occasionally, the lower surface is more or less transversely wrinkled. The younger blades in some taxa may also contain patches of brownish hairs near the base.

In addition to this, there are usually microscopic reddish or orangish glandular punctations, called stegmata by Solereder and Meyer (1928); these stegmata may be prominent, obscure, or absent. In most instances, the nature and distribution of stegmata are useful key characters, but in certain species, such as *C. Yarey*, they are not always diagnostic because stegmata are prominent in some populations and obscure or absent in others. Machado (1945) counted the number of stegmata per square centimeter of leaf in two species of *Copernicia*, and found that *C. alba* had an average of 102 on the dorsal side and 113 on the ventral side, whereas *C. cerifera* had about 20 stegmata on the dorsal surface and 30 to 40 on the ventral surface.

A rachis is evident on the lower surface where the blade and petiole join, and usually varies considerably in size from leaf to leaf of the same tree.

The petiole may be rather short or as long as 160 cm. in *C. tectorum*, or is sometimes absent, as in *C. rigida*, *C. macroglossa*, and *C. longiglossa*. Its upper surface is concave or somewhat flattened; the lower surface is generally convex, and the margins are almost always armed with spine-like teeth of various sizes. Both surfaces may be waxy or non-waxy, or have patches of brownish hairs, and may be with or without stegmata. The petiole-apex is usually much narrower than the base. Whether a petiole is present or not, the leaf-base terminates in an expanded auriculate sheath which may be 30 cm. or more long.

The ligule in *Copernicia* is very variable in size (from 0.5 cm. to about 100 cm. long) and shape (from broadly triangular to long tongue-shaped). It is generally asymmetrical at the base, usually with a concave depression delimiting it from the petiole. The margin is entire, laciniate, or spiny-toothed. In many species the ligule is rather constant in size and shape, but populations of certain species, e.g., *C. rigida* and *C. Baileyana*, show a great range of variability.

Inflorescence and infructescence: Each tree bears several to many inflorescences, each consisting of a many-branched panicle enclosed in a series of overlapping tubular spathes and spathelets. In most species of *Copernicia* the tubular spathelets continue to the last or next-to-last order of branching; however, in some species (*C. cerifera*, *C. tectorum*, *C. gigas*, *C. Berteroana*, and *C. Ekmanii*), the last several orders of branching are generally without tubular spathelets. This is the basis for dividing the genus into the subgenera *Copernicia* and *Copernicia*. Flower-bearing branchlets range from 0.5 cm. to 17 cm. in length and from 0.1 cm. to 1.5 cm. in diameter. Size of flowering and fruiting branchlets is one of the most important diagnostic characters in this genus. Generally, the branchlets become conspicuously evenly or unevenly thickened during fruit

formation, but sometimes they show very little change in diameter. In most species, the flower-bearing branchlets are pubescent, but in *C. glabrescens* and *C. Ekmanii* they are glabrous.

Flowers: Each inflorescence usually bears many flowers. The flowers are bisexual, brownish or yellowish, relatively small (2–8 mm. long), sometimes fragrant (this characteristic seldom has been reported with field data), and usually pubescent. In *C. Ekmanii*, however, they are glabrous, and in *C. glabrescens* they are slightly pubescent or glabrous. Flowers are sessile or subsessile, and solitary or in clusters of two to four. The average distance between flowers or flower clusters varies with each species, and often this is an excellent characteristic for differentiation of taxa. Each flower or flower cluster is subtended by a small variously shaped bracteole from 0.5 mm. to as much as 7 mm. (in *C. macroglossa*) long. When flowers are in clusters, each individual flower is usually subtended by an additional bracteole. Bracteoles are either spreading or folded back, and may be persistent or caducous during fruit formation. The calyx and corolla are campanulate or tubular and each is three-lobed to about the middle. Corolla-lobes are twice or more as long as the calyx-lobes and are usually deeply grooved on the interior. The 6 stamen-filaments are united into a tube; for most of its length this is adnate to the corolla-tube, but at the apex it is free and divided into 6 more or less well-defined lobes which taper abruptly or gradually into short or long appendages which bear the basifixed anthers. The gynoecium is superior and consists of 3 carpels which are distinct below but connate above; each carpel contains one ovule. The ovary is deeply or shallowly three-lobed; the upper surface is pubescent or glabrous, and usually deeply ridged or furrowed, but in *C. alba* the surface is relatively smooth. The single style, which terminates in a simple or obscurely three-lobed stigma, may be completely included in the corolla, as in *C. cerifera*, or exserted, as in *C. alba*.

Fruits: The fruit is formed from only one carpel. It is up to 30 mm. long, ovoid or spherical, usually finely tuberculate, and contains a fibrous exocarp and mesocarp with a thinner leathery endocarp. In most cases, size and shape of fruits are not good diagnostic characters because they are so variable on individual trees. Furthermore, it is often difficult to determine whether fruits are fully mature or not by their external appearance. The solitary spherical or ovoid seed is usually attached at the base of the locule, and exhibits an ovate hilum when it is removed. The exterior of the seed is finely or deeply sculptured. Endosperm tissue is deeply ruminate, and the embryo is basal.

Anatomical studies by Machado (1945) of leaves of two species of *Copernicia* revealed the following differences: in *C. cerifera* the guard cells and stomates are near the leaf-surface, whereas in *C. alba* they are

sunken; and in *C. cerifera* there are about 1.5 times as many stomates per square millimeter of leaf as in *C. alba*. It was also shown that, although stomates were abundant on both surfaces, there were more on the dorsal surface.

In general, the most reliable diagnostic taxonomic characters for *Copernicia* are: degree of waxiness of dried leaf-blades, presence or absence of stegmata, shape of blade-base, size and shape of ligule, size of petiole, distribution of spathelets, size and degree of pubescence of flowering and fruiting branchlets, number of flowers in a cluster, average distance between flower clusters, size and morphology of flowers, and size and shape of bracteoles. When dealing with these characteristics, however, one must consider carefully the range of variation within each species before the taxon can be properly identified.

GEOGRAPHIC DISTRIBUTION

Estimated from our study of the entire genus, *Copernicia* comprises twenty-three species (with one additional variety) and six putative natural hybrids. The genus is confined to the New World, largely in the tropics. Only three species, *C. alba*, *C. cerifera*, and *C. tectorum*, are found on the South American continent; two species, *C. Ekmanii* and *C. Berteroana*, are confined to Hispaniola (Haiti and the Dominican Republic); and the remainder are endemic to Cuba.

It is interesting to note that in South America the distribution of the three species is discontinuous, but that in Cuba many of the taxa have overlapping ranges. This is significant because the South American species seem to be clear-cut, whereas a number of the Cuban species appear to be involved in hybridization.

Because of the complete lack of *Copernicia* fossil material, it would be difficult to trace the origin and migration of this genus.

In the present paper, only the South American species will be considered; a revision of the West Indian taxa will be treated in this journal at a later date. Following a description of the genus *Copernicia* is a key to its species. The taxa are listed in alphabetical order and their treatments include pertinent synonymy, descriptions, lists of specimens examined, and taxonomic and ecological discussions. Economic importance, native names, geographic distribution, and illustrations and distribution maps are also included for each species.

Illustrations of karyotypes of a number of species of *Copernicia* (from root-tips) were prepared by the late Dr. J. Beal of the University of Chicago; unfortunately, collection numbers for all specimens used were

not recorded. The chromosome number for all of the species studied is 2n=36, with no irregularities observed. Fig. 2 illustrates the karyotypes of *C. cerifera* and *C. alba*. No preparations were made for *C. tectorum*.

C. cerifera *C. alba*

2. Karyotypes of two species of *Copernicia*. (Magnification: 2350 ×.)

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Abbreviations used here and elsewhere in the text to indicate the various herbaria are those employed by Lanjouw and Stafleu (1959) in Index Herbariorum:

A	Arnold Arboretum, Cambridge, Mass.
B	Botanisches Museum, Berlin-Dahlem
BH	L. H. Bailey Hortorium, Ithaca, N. Y.
BR	Jardin Botanique de l'État, Bruxelles
C	Botanical Museum and Herbarium, Copenhagen
CHI	University of Illinois, Chicago
E	Royal Botanic Garden, Edinburgh
F	Chicago Natural History Museum
G	Conservatoire et Jardin Botaniques, Genève
G-DC	Herbier De Candolle, Genève
GH	Gray Herbarium of Harvard University, Cambridge, Mass.
L	Rijksherbarium, Leiden
LE	Botanical Institute, Academy of Sciences of the U.S.S.R., Leningrad
LIL	Instituto Miguel Lillo, Tucumán
LP	Museo de La Plata, Argentina
LS	Herbario de la Salle, Habana
M	Botanische Staatssammlung, München
MO	Missouri Botanical Garden, St. Louis
MT	Herbier Marie-Victorin, Montreal
NY	New York Botanical Garden
P	Museum National d'Histoire Naturelle, Paris
PH	Academy of Natural Sciences, Philadelphia
R	Museo Nacional, Rio de Janeiro
S	Naturhistoriska Riksmuseum, Stockholm
SV	Estación Experimental Agronómica, Habana
UC	University of California, Berkeley
VEN	Instituto Botánico, Caracas

TAXONOMY

COPERNICIA Mart., Hist. Nat. Palm. **3**: 242. 1838.

Arrudaria Macedo, Not. Palm. Carnauba 5. 1867.

Trees with straight unbranched trunks covered with persistent petiole-bases for part or all of their length, or smooth, depending on age; leaf-scars usually evident. Petioles elongate or absent, concave or somewhat flattened above, usually convex below, margins armed with spiny teeth of various sizes, surface glabrous or pubescent, waxy or not, with or without stegmata, sheathing base usually auriculate; ligule of various sizes and

shapes, usually asymmetrical, margin entire or laciniate, occasionally spiny-toothed. Leaf-blades fan-shaped, orbicular or cuneiform; blade-segments variable in size and number, elongate, usually with acuminate tips, fused from the base for two-thirds to three-fourths of their length, surfaces with or without coats of wax, stegmata present or absent. Inflorescences several to many on each tree, much-branched, each spadix enclosed by overlapping tubular spathes in a series starting from the base and continuing for some distance along various points of branching; ultimate and penultimate branches of each spadix with or sometimes without tubular spathelets at base. Flower-bearing branchlets variable in length (0.5–17.0 cm.) and diameter (0.1–1.5 cm.), often thickening with the onset of fruit-development, usually pubescent, but occasionally glabrous. Flowers bisexual, brownish or yellowish, inconspicuous (2–8 mm. long), sometimes fragrant, pubescent or occasionally glabrous, solitary or in clusters of two to four; distance between flowers or clusters variable, each flower or cluster subtended by variably shaped bracteoles 0.5–7.0 mm. long. Calyx campanulate or tubular, fused for one-half to two-thirds of its length, three-lobed, lobes usually acute. Corolla tubular or campanulate, longer than calyx, fused for about one-half of its length, three-lobed, the lobes acute or acuminate, interior of lobes usually with 2 or 3 deep grooves. Stamens 6, the filaments connate in a tube largely adnate to the corolla but with 6 free apical lobes terminating in triangular or subulate appendages which bear the anthers; anthers ovate or oblong, attached near their base, 0.2–1.2 mm. long. Pistil of 3 more or less united uniovulate carpels; ovary superior, ovoid or somewhat obovoid, more or less clearly three-lobed, usually furrowed or ridged on upper surface; style one, included or exserted from corolla, stigma indistinctly three-lobed or simple. Fruit ovoid or spherical to 30 mm. long, more or less finely tuberculate, mesocarp fibrous, endocarp leathery, seed one, ovoid or spherical, sculptured, to 20 mm. long, attached at base of endocarp, endosperm deeply ruminate, embryo basal. (*Copernicia*, after the astronomer Nicolaus Copernicus, 1473–1543.)

Type species: *Copernicia cerifera* (Arruda da Camara) Mart. (*Corypha cerifera* Arruda da Camara).

KEY TO SOUTH AMERICAN SPECIES

1. Flower-bearing branchlets of each panicle with tubular spathelets usually to the last order of branching (Subgenus Copernicia), 3–7 cm. long; flowers 5–6 mm. long. ..... 1. *C. alba*

1. Flower-bearing branchlets of each panicle without tubular spathelets (Subgenus Copernicia), 4–17 cm. long; flowers 3–3.5 mm. long.

   2. Flowers solitary, subtended by ovate bracteoles; calyx mostly shallowly lobed; flowering and fruiting branchlets up to 17 cm. long; leaf-blades not waxy, stegmata prominent. ..... 2. *C. tectorum*

   2. Flowers in clusters of 2–4, subtended by fimbriate bracteoles; calyx usually deeply lobed; flowering and fruiting branchlets up to 12 cm. long; leaf-blades usually densely waxy, stegmata obscure or evident, but usually not prominent. ..... 3. *C. cerifera*

Subgenus COPERNICIOPSIS Becc., Webbia **2**: 144. 1907.

Branchlets of each panicle with tubular spathelets to the last or next-to-last order of branching.

Type species: *Copernicia alba* Morong.

1. **Copernicia alba** Morong, Ann. N. Y. Acad. Sci. **7**: 246. 1893

Copernicia cerifera Mart., Hist. Nat. Palm. **3**: 242. pl. 50A. 1838, pro parte; Morong, Ann. N. Y. Acad. Sci. **7**: 245. 1893; non Arruda da Camara, 1810.
Copernicia rubra Morong, Ann. N. Y. Acad. Sci. **7**: 247. 1893.
Copernicia australis Becc., Webbia **2**: 158. 1907.
Copernicia nigra Morong ex Becc., Webbia **2**: 158. 1907, pro syn.
Copernicia australis var. *alba* (Morong) Bertoni ex Hauman, Physis **4**: 607. 1919.
Copernicia australis var. *nigra* (Morong) Bertoni ex Hauman, Physis **4**: 607. 1919.
Copernicia ramulosa Burret, Notizbl. Bot. Gart. Berlin **10**: 403. 1928.

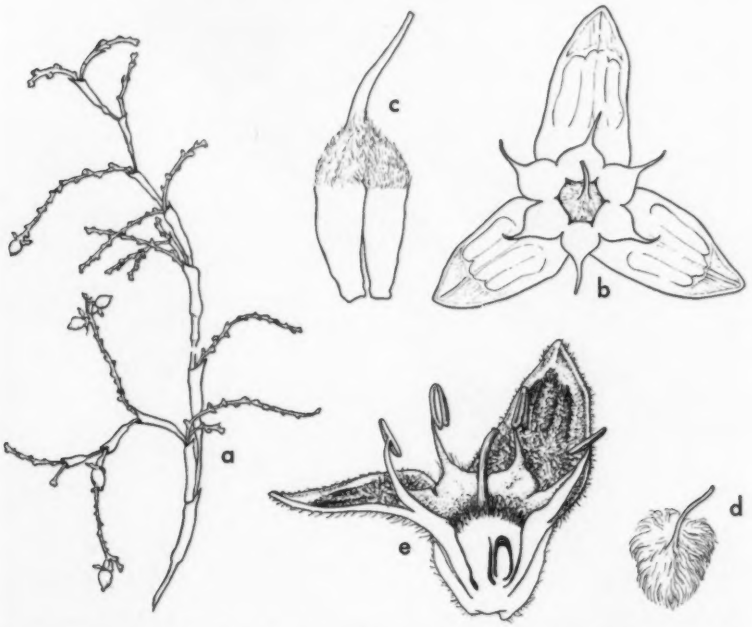
Tree 8–30 m. tall (*fide* Michalowski), trunk 17–22 cm. in diameter. Younger trees with persistent petiole-bases, older trunks mostly smooth to the base. Petioles up to 78 cm. long, to 2.4 cm. wide at apex, and to 4.8 cm. wide at base, upper third or half mostly with entire margins, lower half or two-thirds with coarse, irregularly spaced spiny teeth up to 2 cm. long, the sheathing base up to 32 cm. long and 14 cm. wide; ligule 1.2–2.5 cm. long (measured from base of one side to apex), ovate, margins usually entire. Leaf-blades orbicular; blade-segments about 48 in number, the central one to 76 cm. long, usually densely waxy and with prominent orange or reddish stegmata on both surfaces. Inflorescences about 1.8 m. long, primary spathes glabrous. Flowering branchlets densely pilose, 3–7 cm. long, 1–1.5 mm. in diameter, spathelets usually pilose only on the tips and margins. Flowers 5–6 mm. long, in clusters of two, the clusters about 1.5–3 mm. apart, subtended by acute or acuminate bracteoles 2–4 mm. long; calyx densely pilose, 2.5 mm. long; corolla densely pilose on exterior, lobes 3.5 mm. long, narrowly triangular; terminal anther-bearing appendages of stamen-ring with broad base 1 mm. long and subulate terminal portion 1 mm. long, anthers 0.75–1.20 mm. long; ovary obpyriform, not furrowed, densely pubescent on upper one-half to two-thirds, style 2 mm. long, exserted from the corolla. Fruit ovoid, to 20 mm. long and 17 mm. in diameter, seed about 14 × 12 mm. (Plates I and III; Figs. 2 and 3–10.)

Flowering occurs from May through February.

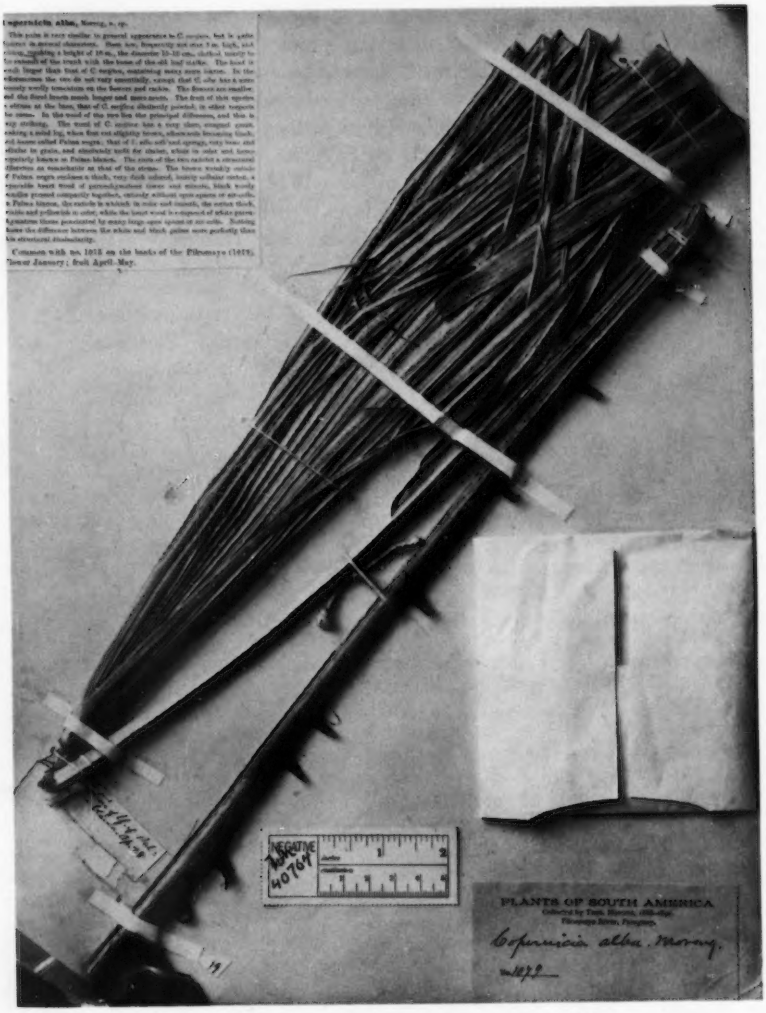
Type: Banks of Pilcomayo River, Paraguay, Morong 1079 (NY).

Distribution: Western Matto Grosso (Brazil), eastern Bolivia, most of Paraguay, and the northern one-fourth of Argentina. Martius (1844) says that this palm is very common along Río La Plata (probably in Uruguay), and Croizat (1952) lists the genus *Copernicia* from Uruguay. No other literature or specimens have been seen to corroborate these reports. Perhaps this entry refers to *Trithrinax campestris* (Burmeist.) Drude & Griseb., which was originally described as a species of *Copernicia* by Burmeister (see EXCLUDED SPECIES). Some of the more recent articles, e.g., Castellanos and Ragonese (1949), list *T. campestris* from Uruguay, but no species of *Copernicia* is mentioned.

Vernacular names: Caranday, carandá. See Dahlgren (1936) for a more complete list of names. Another palm, *Trithrinax campestris*, is also called caranday in Argentina.



3. *Copernicia alba*. a, inflorescence, showing branchlets with tubular spathelets; b, flower, face view (anthers missing); c, pistil; d, top of ovary and style; e, longitudinal section of flower, showing stamen-ring with long filaments and relatively long style. (a, b, c, d: *Markley & Kitzke P 10* [F]; e: *Castellanos 3304* [BH].)


Copernicia alba, Morong, n. sp.
Common with no. 1015 on the banks of the Pilcomayo (1079).
Flower January; fruit April–May.
NEGATIVE No. 40769
PLANTS OF SOUTH AMERICA
Copernicia alba. Morong.
1079

4. Type of *Copernicia alba. Morong 1079* (NY).

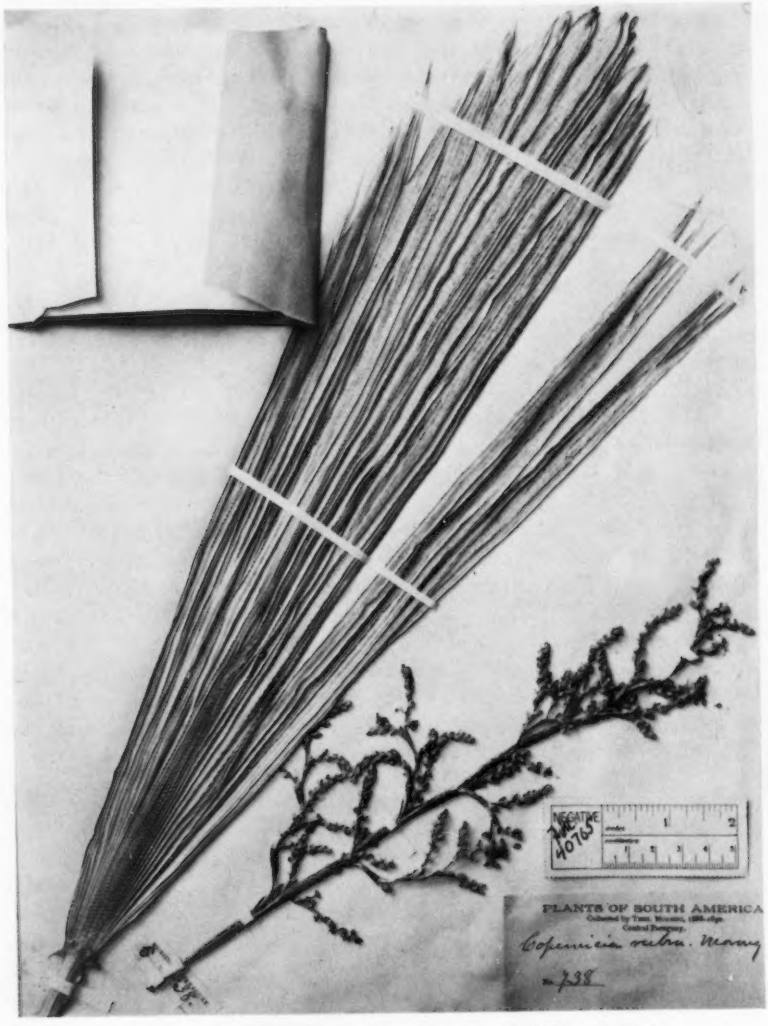
ARGENTINA. Chaco: Colonia Benítez a Antequeras, *T. Meyer 2104, 2334, 9072* (LIL); Machagay, *T. Meyer 9857* (LIL). Corrientes: Las Mercedes, *Cabrera 10537* (LP). Jujuy: El Palmar, *Cabrera 4075* (F, LP). Santa Fe: Palmar La Juana, *Ragonese 2393* (BH); Estancias Las Camelias, *Ragonese 2646* (BH); between Malabrigo and Berna, *Ragonese 2649* (BH, LP); between Río Calchaquí and Laguna El Palmar, *Ragonese 3033* (BH); Los Amores, *Ragonese 3304* (BH, LP). Province undetermined: [without locality] *Lorentz & Hieronymus s. n.* (S); Tuyuyu, *Morel 7678* (G); Estancia Yacare, *Pierotti 6* (S); Posta San Martín, *Pierotti 4103* (LIL); Punta Pora (Tres Lagunas), *Rojas 8987* (LP).

BOLIVIA. Between Limoquije and Trinidad, *Werdermann 2227* (S).

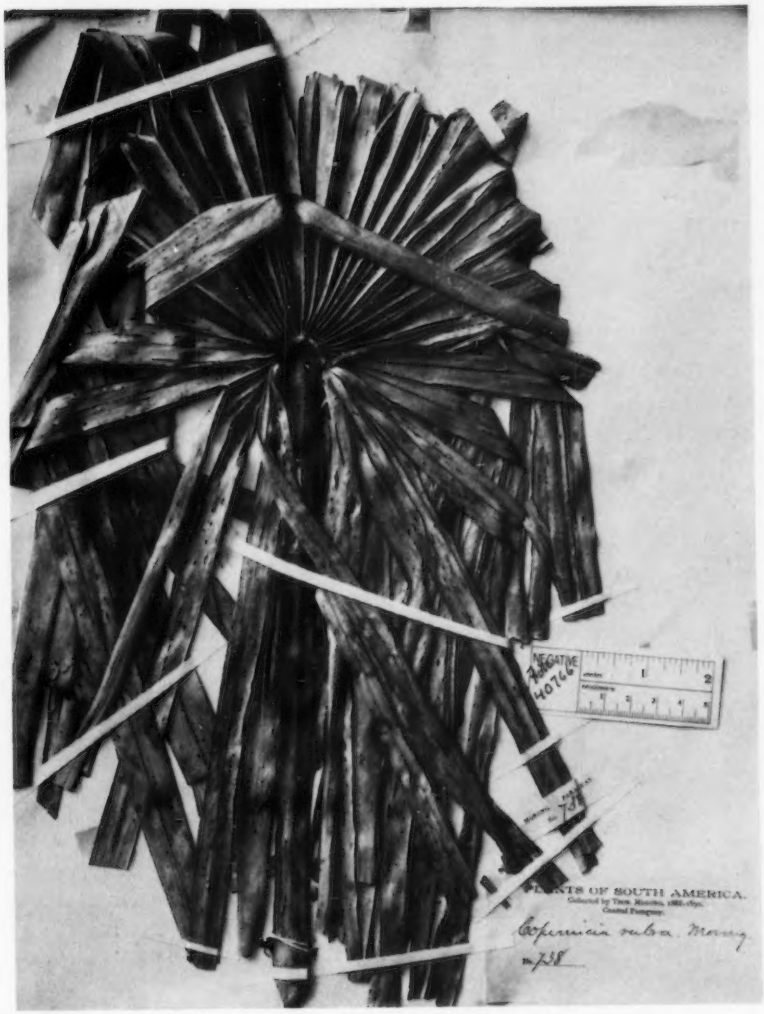
PARAGUAY. Guarní, *Balansa 2714* (P); between Río Apa and Río Aquidabán, *Fiebrig 4429* (E, G, GH, L, M, isotypes of *C. ramulosa*); campis humidis pr. Tugueri, *Hassler 1481* (B, G, NY, P); Río Apa, *Hassler 11524* (A); region of Lake Ypacaray, *Hassler 12393* (C, G, GH, L, MO, NY, S, UC, paratypes of *C. ramulosa*); Tugueri, *Herter 7704* (L); [without locality] *Kuntze s.n.* (BH); El Chaco, *Lindman s.n.* (S); Estancia Estrella, *Markley & Kitzke 2* (F); Río Salado, *Markley & Kitzke 3, 4, 8* (F); Estancia La Bella, *Markley & Kitzke 7, 8, 9* (F); Puerto Guaraní, *Markley & Kitzke P 10, P 11, P 12, 23, 32, 34, 36* (F); Puerto Casado, *Markley & Kitzke P 18, P 19, P 20, 20, 22, 24* (F); Estancia Deolinda, *Markley & Kitzke 53/061, P 24* (F); Puerto Casado, *McLoud 405275* (F); Trinidad, *T. Meyer 287* (LIL); Pilar, near mouth of Río Bermejo, *T. Meyer 16106* (LIL); central Paraguay, *Morong 738* (MO, NY, paratypes of *C. rubra*); central Paraguay, *Morong 1073* (GH, MO, NY, PH); Pilcomayo River, *Morong 1078* (NY, type of *C. rubra*; G, GH, MO, PH, isotypes); banks of Pilcomayo River, *Morong 1079* (NY, holotype—one sheet, leaf and fruits; MO, isotype); Gran Chaco, Fort Bourbon, *Weddell 3200* (P).

CULTIVATED. Botanical Gardens, Rio de Janeiro, Brazil, *Bailey 425a* (BH) and *H. Johnstone 1780* (B).

In both 1824 and 1838, Martius erroneously included this species under *C. cerifera*. His plate 50A is an illustration of what is now known as *C. alba*. He also mentioned Paraguay and Bolivia as part of the distribution of *C. cerifera*. Morong, in 1893, described two new species of *Copernicia* from Paraguay, as distinct from a third species which he, also, incorrectly thought to be *C. cerifera*. He said that *C. cerifera* was known as "palma negra," *C. alba* as "palma blanca," and *C. rubra* as "palma colorada." Morong distinguished these three taxa by size of the tree, color and texture of the wood, degree of pubescence of the inflorescence-branches and



5. Type of *Copernicia rubra. Morong 738* (NY), sheet 1.



6. Type of *Copernicia rubra. Morong 738* (NY), sheet 2.

7. *Copernicia alba.* The type recognized as "palma blanca" by natives in Paraguay. Between Puerto Guaraní and Puerto Casado. (Photograph by E. D. Kitzke.)

8. *Copernicia alba.* Another type, recognized as "palma colorada" by natives in Paraguay. Between Puerto Guaraní and Puerto Casado. (Photograph by E. D. Kitzke.)

9. *Copernicia alba*. The third type, recognized as "palma negra" by natives in Paraguay. Between Puerto Guaraní and Puerto Casado. (Photograph by E. D. Kitzke.)

flowers, size of flowers and flower-bracteoles, and several other characters. After studying numerous specimens, including mass collections of Markley and Kitzke from Paraguay, we have concluded that the three "species" in question are actually different stages of growth and maturation of one taxon. *Copernicia alba* represents the younger trees with whitish wood, *C. rubra* the intermediate stages with reddish wood, and *C. cerifera* (Morong, not Martius) the mature trees with blackish wood. This agrees with the conclusions of several other botanists who have previously worked on this problem. In 1907, Beccari described this assemblage as *C. australis*, a name, however, which becomes a synonym because of the existence of the earlier available name. Later, Britton (1908) pointed out that, according to the rules of nomenclature, Beccari should have used one of Morong's names even though all three belonged to one species. This situation was not settled, however, until 1942, when Ragonese and Covas assigned both Morong's and Beccari's epithets to synonymy under *C. alba* Morong, which now is the valid name. In 1928, Burret described another species from Paraguay, *C. ramulosa*. He distinguished this taxon from *C. alba* primarily by the last order of panicle branches' being without tubular spathelets. In fact, Burret considered this palm a link between

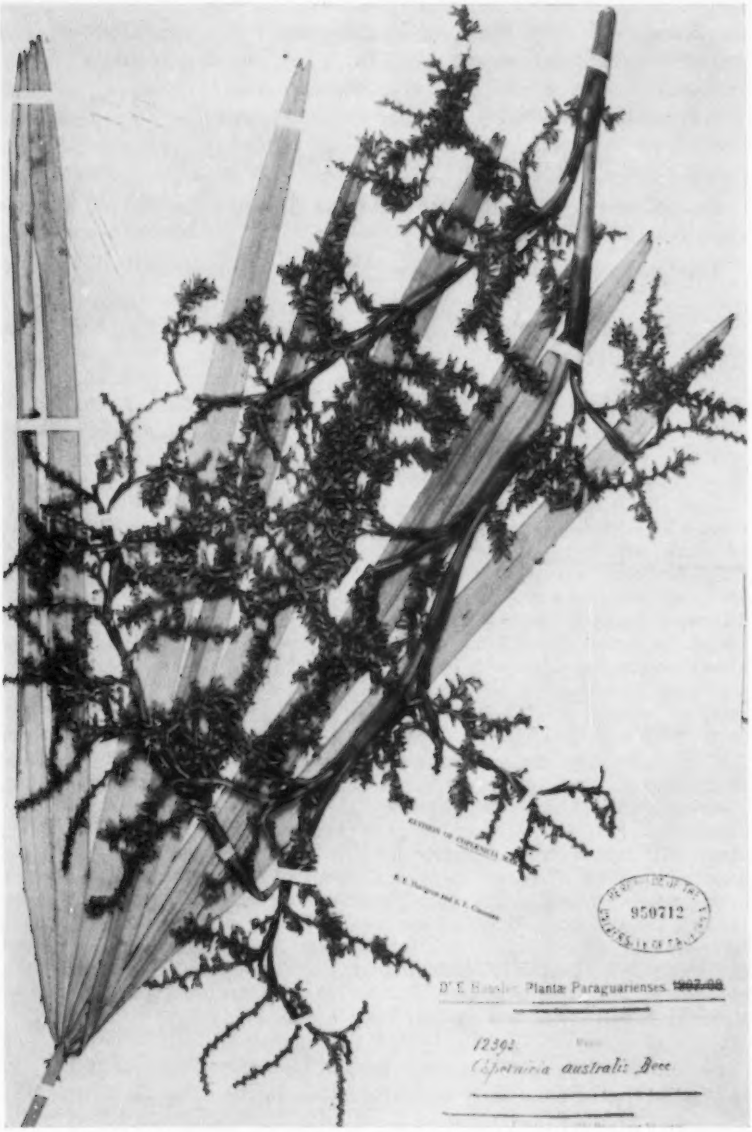
the two subgenera of *Copernicia*, *Eucopernicia* [= *Copernicia*] and *Copernicioopsis*. We have studied many specimens of *C. alba* and have found this character to be very variable. On a number of specimens examined, last-order branchlets are either with or without tubular spathelets on the same inflorescence; therefore, we do not consider *C. ramulosa* to be a distinct species.

According to Michalowski (1958), *Copernicia* palms of western Brazil and Paraguay are distributed by size as follows: in Matto Grosso and northern Paraguay (on the borders of the Paraguay River between Puerto Sastre and Fuerte Olimpo), the trees are 25 to 30 m. tall; between Río Aquidibán and Río Apa and extending through the Chaco toward Bolivia, they range from 15 to 20 m. tall; and in the central region, and southern region of Pilar, the trees are only 8 to 15 m. in height.

Apparently, *C. alba* is the most abundant species of *Copernicia*. From aerial photographic surveys, Markley (1955) found that in the northeastern section of the Paraguayan Chaco above Bahía Negra, and extending into Bolivia and Brazil, this palm occurs in solid stands hundreds of square miles in extent. It was estimated that the largest stands in this region alone contained about a half-billion palms. Markley also estimated that the entire population of *C. alba* was ten times or more as great as the population of *C. cerifera* in Brazil. Ragonese and Covas (1942) mention excellent stands of *C. alba* for Argentina in the estancias Camelias and Goldara near Reconquista in Santa Fe province, and in the vicinity of El Tigre on the border of the provinces of Santa Fe and Chaco; and Jones (1930) says there are isolated groups of these palms on wet clay soils in Lagunas del Iberá, in Corrientes province.

For the most part, *C. alba* is found in areas subject to periodic flooding followed by complete drainage and later to a period of drying of the soil surface. This palm does not usually occur in regions above the flood level or where the land is submerged by water more or less continuously. Apparently, water is the primary agent for fruit dispersal, but cattle, which eat the fruit, are also responsible for spreading the plant by regurgitation of the seeds. Frequent burning of adjacent grasslands also enables this palm to spread (Markley, 1955).

Although the wax from leaves of *C. alba* is generally of high quality, it has not been exploited commercially to a large degree, mainly because of the labor shortage (Markley, 1955). Workers who live in the regions where the palms grow are generally employed by quebracho-processing plants, a year-round operation which is probably more profitable than would be the production of wax. Markley also discusses other considerations for wax production. Ragonese and Covas (1942) mention the following uses of *C. alba* for Argentina: the trunks are frequently used for tele-



10. Isotype of *Copernicia ramulosa. Fiebrig 4429* (UC).

phone poles, for posts for barbed-wire fences, and in the construction of dwellings, and the leaf fibers can be employed in the manufacture of hats and as a horticultural mulch.

Subgenus COPERNICIA

Subgenus *Eucopernicia* Becc., Webbia **2**: 143. 1907.

Flower- and fruit-bearing branchlets of each panicle without tubular spathelets.

Type species: *Copernicia cerifera* (Arruda da Camara) Mart.

2. **Copernicia cerifera** (Arruda da Camara) Mart., Hist. Nat. Palm **3**: 242. 1838.

Corypha cerifera Arruda da Camara, Discurso Util. Inst. Jard. 1810.
Arrudaria cerifera (Arruda da Camara) Macedo, Not. Palm. Carnauba: 5. 1867.

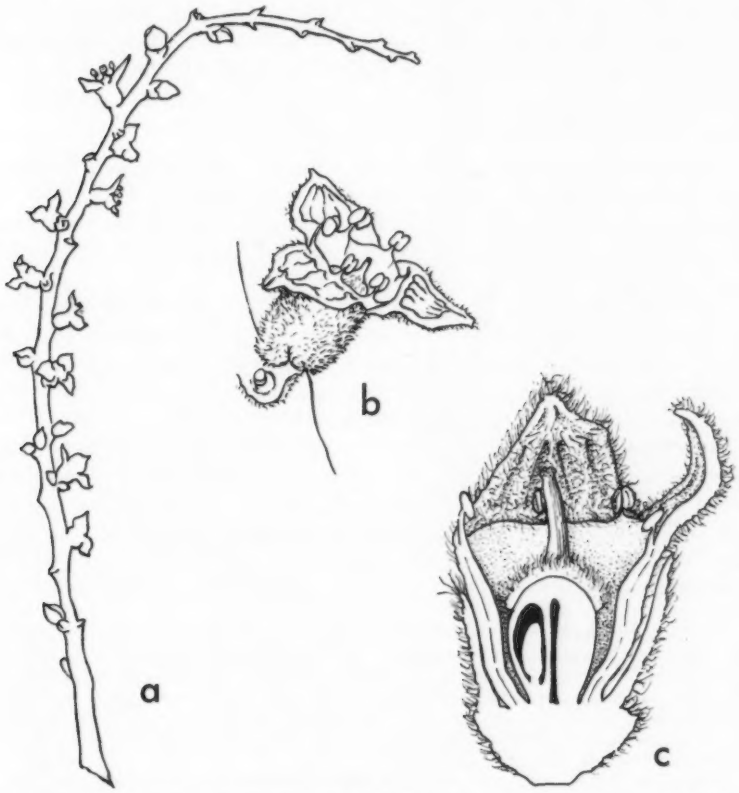
Tree 10–15 m. tall (*fide* Taube), trunk 15–25 cm. in diameter. Younger trees with sheathing petiole-bases persisting on about two-thirds the length of trunk; petiole-bases abscissing and leaving noticeable leaf-scars as trees reach maturity, except in lower 3 m. or so of trunk which has permanently attached petiole-bases. Petiole up to 115 cm. long, margins armed with coarse, irregularly spaced spiny teeth up to 1 cm. long, sheathing base 25–35 cm. long; ligule 2–5 cm. long (measured from base of one side to apex), ovate, margins entire or laciniate. Leaf-blades orbicular; blade-segments in immature trees 35–45 in number, in mature trees 58–62 in number, central one 60–93 cm. long, usually densely waxy on both surfaces, with stegmata obscure or evident, but not prominent. Inflorescences 1.5–2.7 m. long, primary spathes glabrous. Each panicle-branch consisting of five to seven secondary branchlets which are without tubular spathelets. Flowering branchlets densely pilose, up to 12 cm. long, 1.5–2.5 mm. in diameter. Flowers 3–3.5 mm. long, in clusters of two to four, the clusters about 2–3 mm. apart, subtended by two fused fimbriate bracteoles 1–2.5 mm. long; calyx pilose on exterior, 2 mm. in diameter; corolla pilose on exterior, lobes broadly triangular; stamen-ring with 6 very short anther-bearing appendages, the anthers about 0.25 mm. long; ovary broad, furrowed or ridged above, scattered-pilose on upper surface, otherwise glabrous; style short and thick, included in the corolla, stigma shallowly three-lobed. Fruit ovoid, up to 27 mm. long, 22 mm. in diameter, seed up to 20 × 17 mm. (Plates I and II; Figs. 2 and 11–14.)

Flowering occurs from January through December.

Distribution: Found only in northeastern Brazil, from Rio Pindare in Maranhão on the west to beyond Rio Assu in Rio Grande Do Norte on the east, northward to the coast and southward at least to Rio Santo Antônio

in Baía. St. Hilaire (1822) and subsequent authors mention carnauba from the state of Goyaz, but according to surveys made by S. C. Johnson & Son, Inc. and Luetzelburg (1923), and judging from the absence of specimens from that area, there are no authentic records for that state. Teixeiro da Fonseca (1927) lists *C. cerifera* from the state of Pará, but there are only cultivated specimens to substantiate this report. Martius (1844) says that this species is common in the Amazon region, but according to Le Cointe (1934), it is cultivated in the Brazilian part of that region.

Vernacular names: Carnauba, carnauva, carnaiba, carnahyba, carnaubeira, carandauba.



11. *Copernicia cerifera*. a, portion of inflorescence branchlet; b, a single flowers c, longitudinal section of flower, showing stamen-ring with short filament; and short style. (a, b: *Dahlgren 46/026;* c: *Bailey 448* [BH].)

BRAZIL. Baía: Marais de St. Antoine, *Blanchet 3152* (G-DC, neotype—two sheets, inflorescence and leaf; NY, P, isoneotypes); [without definite locality] *Martius s.n.* (M); Joazeiro, *Rose & Russell 19765* (NY). Ceará: [without definite locality] *Fr. Allemão de Cysneiros 1565* (R); Fortaleza, *Dahlgren 615038* (CHI, F); Barroso, Municipio de Aquiraz (near Fortaleza), *Dahlgren s.n.* (F); Raposa, *Kitzke 55/117* (F). Pernambuco: Campis ad Rio São Francisco, *Martius s.n.* (C); [without definite locality] *Martius s.n.* (M), *Werdermann 2936* (B). Piauí: Marais de Tapera, *Blanchet 3085* (G-DC); São Pedro de Alcântara, *Schwacke 220, 975* (R).

CULTIVATED. Hort. Mus. Pará, *Burret s.n.* (B); Botanical Garden, Rio de Janeiro, *Glaziou 9016* (C, LE, P); Castleton Gardens, Jamaica, *Bailey 15031* (BH); Botanical Garden, Georgetown, British Guiana, *Bailey 448* (BH), *Dahlgren 610702* (F); U. S. Plant Introduction Gardens, Chapman Field, Florida, *Dahlgren 52/092* (F). According to Le Cointe (1934), this species is also cultivated in the Amazon region of Brazil.

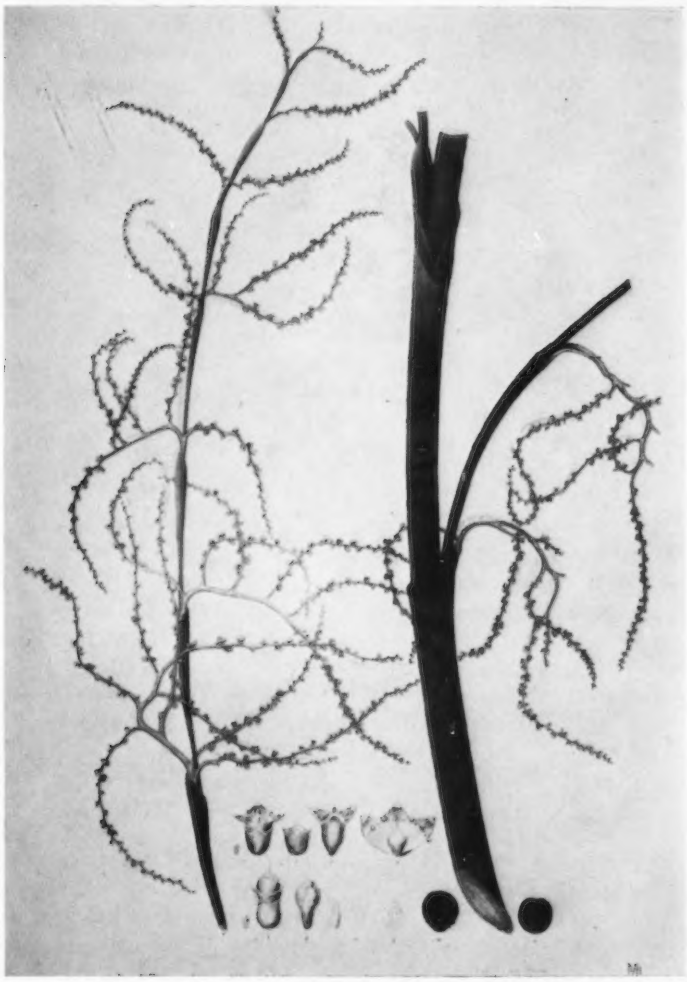
Apparently, the first published reference to this palm and the first recorded spelling of its vernacular name ("caranaiba") were those of Marcgravius and Piso (1648). In a later work, Piso (1658) illustrated this plant (see Fig. 13). Today, this species is generally known as "carnauba" over most of its range.

In the "*Discurso*" by Arruda da Camara (1810), the author states that J. M. C. Velloso published in a periodical called *Palladio Portuguez*, in 1797, an account of Arruda da Camara's discovery of this palm's potentialities as a source of wax. As we are unable to locate this publication, it is not clear whether Velloso actually named *C. cerifera* or whether he merely made reference to it by common name.[1] In addition, no specimens have been found pertaining to this matter. It seemed logical to choose a neotype from one of Martius' collections, but two of his specimens were eliminated from consideration because there were no leaves. In the other specimen from Baía, with both flowers and leaves, the stegmata are prominent and encircled by a red outline. This feature is not characteristic

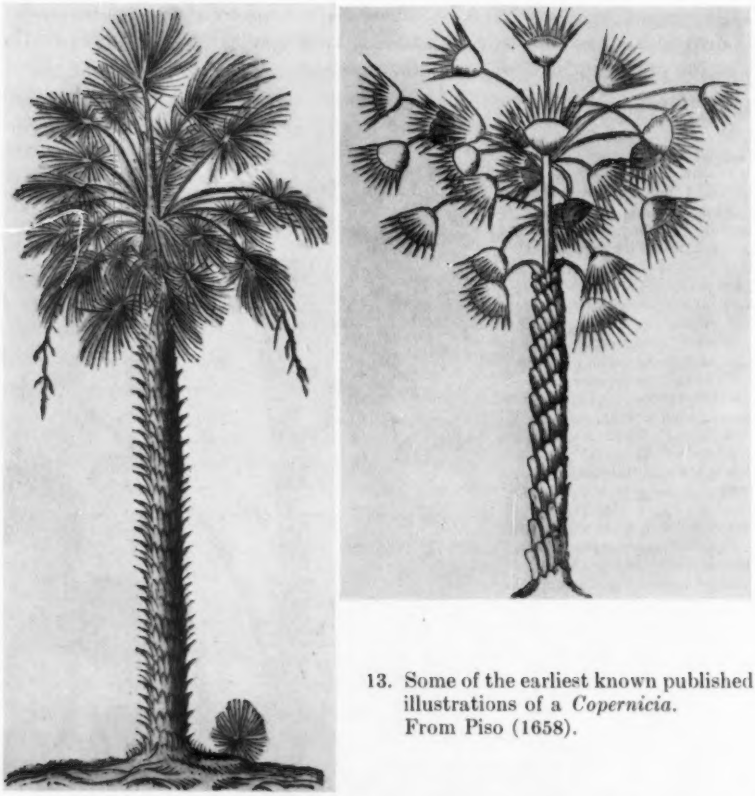
[1] [Editor's note—According to the *Grande Enciclopedia Portuguesa e Brasileira* **20:** 37 (1945), the journal *Palladio Português* (sic) was published at Lisbon from 1796 to 1797. Attempts to locate copies in this country have failed, and inquiry at the Biblioteca Nacional de Lisboa, Portugal, has revealed that it possesses only Volume 1 (1796), incomplete. However, it seems unlikely that the account of the carnauba palm, published in this work by Velloso (Vellozo, Velozo) according to Arruda da Camara, would affect the nomenclature of this species.

Arruda da Camara's accounts of *Corypha cerifera* and other plants in the "*Discurso*" also contain reference to "*Arrud. Cent. Plant. Pern.*" This is the work listed by Pritzel as "261. **Arruda da Camara,** *Manoel.* Centuriæ plantarum pernambucensium, quas *Martinus Ribeiro* (†1816) delineaverat, ineditæ." As Pritzel indicated, this appears never actually to have been published.]

of *C. cerifera*, and may be an abnormality due to the way the leaf was dried. Blanchet 3152 is the most characteristic of the older collections, in the opinion of the authors, and therefore has been chosen as a neotype.



12. *Copernicia cerifera*. Inflorescence, showing individual branchlets without tubular spathelets. From Martius (1824).



13. Some of the earliest known published illustrations of a *Copernicia*. From Piso (1658).

In both 1824 and 1838, Martius included two species in his treatment of *C. cerifera*. His Fig. 50 is *C. cerifera*, but Fig. 50A is what is now called *C. alba*.

Taube (1952) estimates the number of carnauba trees in northeastern Brazil to be 100 million or more, the largest stands occurring in the states of Piauí and Ceará. The trees are abundant along banks of rivers and streams and also fringe the borders of shallow lake basins. During the rainy season (January to June), the rivers, streams, and lakes overflow their banks, whereas in the dry season they are almost entirely without water. Occasionally, there are drought periods of one to several years' duration, during which the rainfall drops far below the annual average of forty-five to fifty inches. Throughout the year the temperatures average around 80° F.

Carnauba trees grow very slowly. A tree must be at least ten years old before it yields wax in appreciable quantities. According to Taube (1952), these palms frequently live to be one hundred years old and occasionally one may reach an age of two hundred years; however, Kitzke

14. *Copernicia cerifera*. A stand along the Rio São Francisco near Remanso, Brazil. From Karsten and Schenck (1908).

(personal correspondence) states that this is an error which has been perpetuated from the early literature. From field studies made at the Raposa plantation in Ceará where leaves of these palms have been harvested for wax, Kitzke concludes that 75 years would be very ancient for carnauba trees. In fact, he judges that a palm allowed to grow without leaf-harvesting might be even shorter-lived than one which is regularly harvested. Taube also discusses the history and commercial importance of carnauba wax. Many other articles have been written on the importance of carnauba wax, but they are too numerous to cite here. A list of such references can be obtained from Dahlgren (1936) and from S. C. Johnson & Son, Inc., Racine, Wisconsin. Besides wax, the leaves also yield fibers which are used in making hats, baskets, and mats. The wood is used in construction of fences, houses, and bridges because it is resistant to insect attacks and can withstand the effects of salt water.

3. **Copernicia tectorum** (H.B.K.) Mart., Hist. Nat. Palm **3**: 243. 1838.

Corypha tectorum H.B.K. Nov. Gen. et Sp. Pl. **1**: 299. 1816.
Copernicia sanctae-martae Becc., Webbia **2**: 154. 1907.

Tree up to 10 m. tall (*fide* Beccari), trunk 25–30 cm. in diameter. Younger trees with persistent sheathing petiole-bases; mature trunks mostly smooth to the base. Petiole up to 158 cm. long, about 2 cm. wide at apex, 5.5 cm. wide at base, margins armed with coarse spiny teeth up to 2 cm. long, sheathing base 15–24 cm. long; ligule 1.5–4.5 cm. long (measured from base of one side to apex), usually asymmetrical, truncate or rounded, margins entire or sometimes laciniate. Leaf-blades orbicular; blade-segments about 40 in number, central one up to 98 cm. long, green on both surfaces, with prominent orange or whitish stegmata on both surfaces. Inflorescences about 1 m. long, primary spathes glabrous; each panicle-branch consisting of eight to twelve secondary branchlets which are without tubular spathelets. Flowering branchlets densely pilose, up to 17 cm. long, 1–2.25 mm. in diameter. Flowers 3–3.5 mm. long, solitary, about 1–3 mm. apart, each subtended by an ovate bracteole 0.25–0.50 mm. long which usually falls off during maturation of fruit; calyx pilose on exterior, 2 mm. in diameter, shallowly lobed, more or less truncate at base; corolla pilose on exterior, lobes usually broadly triangular; stamen-ring with six very short anther-bearing appendages, anthers about 0.4 mm. long; ovary broad, furrowed or ridged above, minutely pilose on ridges, otherwise glabrous; style short and thick, included in the corolla, stigma not lobed. Fruit ovoid, up to 28 mm. long and 20 mm. in diameter, seed up to 14 × 12 mm. (Plates I and IV; Figs. 15–21).

Flowering occurs in January and February.

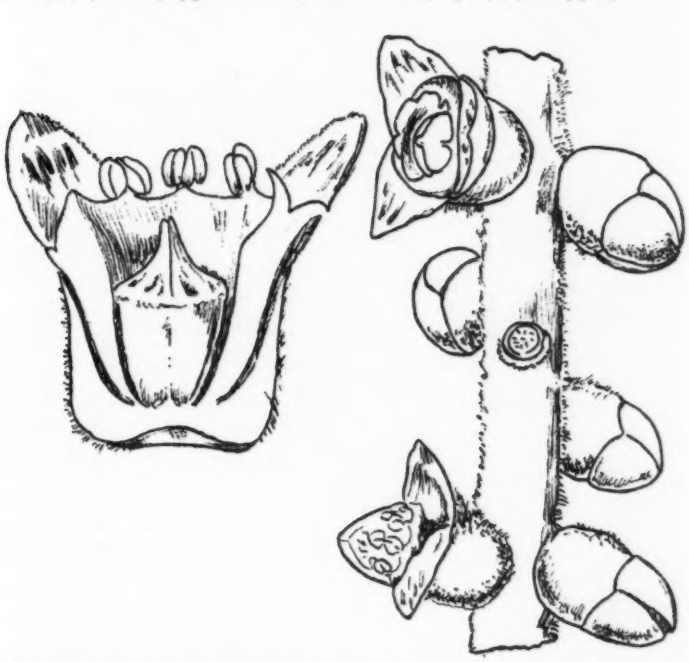
Type: In vasta planitie Caracasano-Cumanesi, *Bonpland 796* (P).

Distribution: In savannas of north-central Venezuela from about Caracas to Cumaná, from the coast to the Orinoco River; and in swampy

lowlands subjected to intermittent and extended dry periods along and near the central coast of Colombia, from approximately Santa Marta to Cartagena. Grisebach (1864) erroneously reported *C. tectorum* from Haiti and Jamaica. According to Britton (1908) and Moscoso (1945), this species does not occur on Haiti; and Bailey (1938) says that the Jamaican *Copernicia* is based on a *Thrinax* and a *Bactris*. The report from Haiti is probably based on a similar native species of *Copernicia*, namely *C. Berteroana*.

Vernacular names: Cobija, palma de cana, palma de sombrero, palma llanera (Venezuela). Palmiche, palma sarra, palma redonda (Colombia).

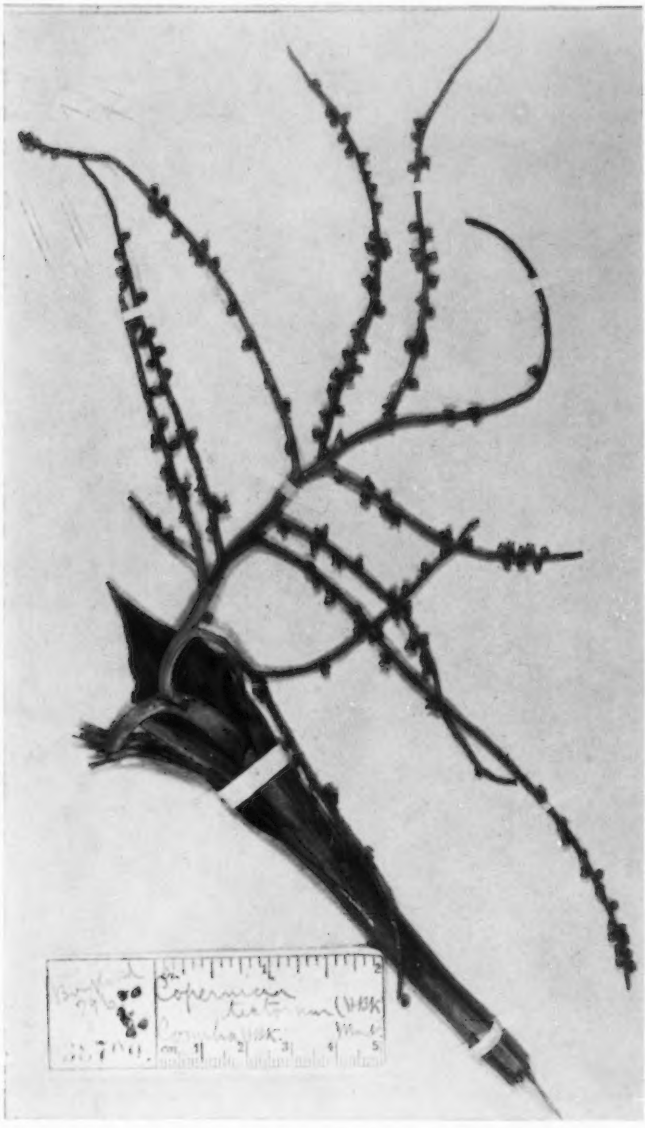
COLOMBIA. Atlántico: Near Cartagena, along Baranquilla Rd., *Bailey 240* and *254* (BH); near Ponedera, *Dugand 299* (CHI); near arroyo de Piedras, Laguna de Guájaro, *Dugand 2825* (CHI). Magdalena: Ciénaga, *Foster & Earle Smith 1628* (BH); Ciénaga Grande, opposite Baranquilla, *P. Hershkowitz 404918* (F); Santa Marta, border of Río Magdalena, *L. Schlim 954* (G-DC, type of *C. sanctae-martae*; G, L, P, isotypes).



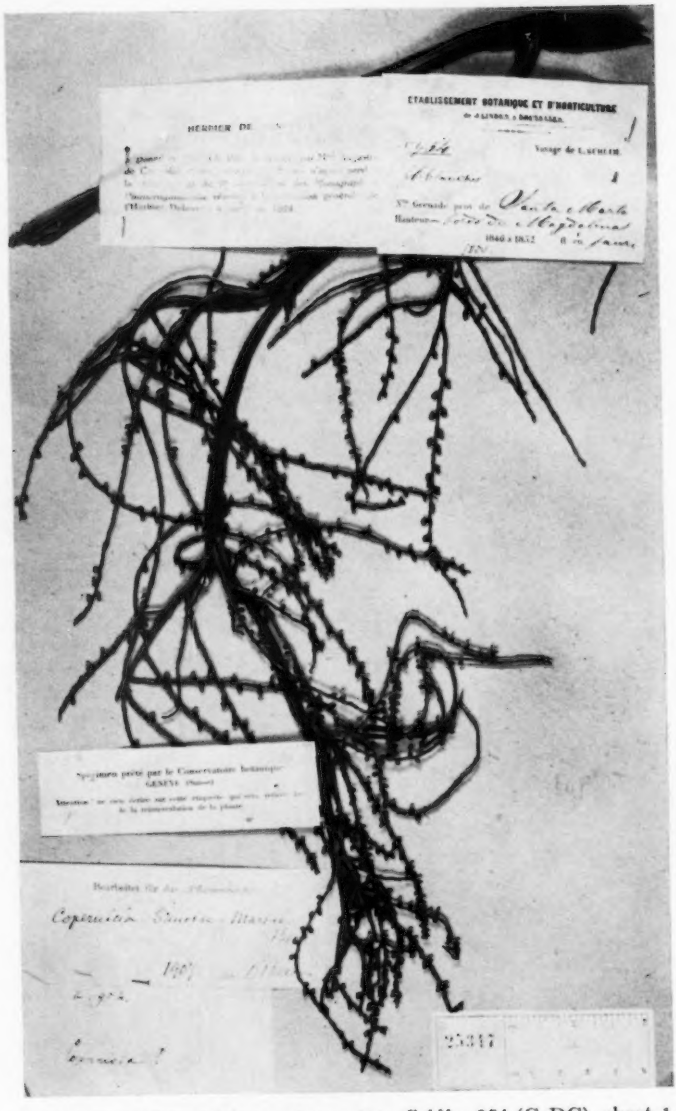
15. *Copernicia tectorum*. Portion of a flower-bearing branchlet, and a single flower. After Beccari (1931).

VENEZUELA. Bolívar: Savanna outside of Caicara, *L. Williams 13275* (CHI, F, G). Guárico: Palmar de Santa Rosa, *Chardon 232* (VEN); Santa María de Ypire, *Brother Gines s.n.* (F); between Ortiz and El Sombrero, *Pittier 11302* (GH, VEN); between El Sombrero and Chaguaramas, *Tamayo 3504* (VEN); El Sombrero, *G. Woronov 7275* (LE). [Exact state unknown]: In vasta planitie Caracasano-Cumanesi, *Bonpland 796* (P, photograph of type; M, isotype—fragment of inflorescence).

16. *Copernicia tectorum*. Fruits and seeds. *Hershkowitz 49/102*.



17. Type of *Copernicia tectorum*. *Bonpland 796* (P).



18. Type of *Copernicia sanctae-martae. Schlim 954* (G-DC), sheet 1.

19. Type of *Copernicia sanctae-martae. Schlim 864* (G-DC), sheet 2.

CULTIVATED. Boldingh (1914) reports that *C. tectorum* is cultivated in the Dutch West Indies. The following specimens were seen by us from Curaçao, one of these islands: *Britton & Shafer 3000* (GH, MO, NY, S); *Curran & Haman 176* (A).

When Beccari originally described *C. sanctae-martae*, he distinguished it from *C. tectorum* by its having conical-acute flower buds, petals longer than wide, and corolla six-ribbed internally, rather than spherical flower buds, petals as long as wide, and corolla smooth within. After studying a large number of specimens from both Colombia and Venezuela, we have concluded that these characteristics are too variable to be valid criteria for separating two species. In this connection, Dugand (1955) thinks that

20. *Copernicia tectorum*. Stand of trees near Caicara, Venezuela. (Photograph by Llewellyn Williams.)

21. *Copernicia tectorum*. Stand of trees near Barranquilla, Colombia. (Photograph by P. Hershkowitz.)

C. sanctae-martae is probably only a variety of *C. tectorum*. We feel, however, that they represent one variable but not readily subdividable taxon even though the populations are discontinuously distributed, in Colombia and Venezuela.

According to Hershkowitz (personal correspondence), this palm is especially abundant, forming extensive stands in the vicinity of Ciénaga Grande de Santa Marta in Magdalena and Ciénaga de Luruaco in Atlántico. The pH of the soil in the first region ranges between 8 and 9. According to Croizat (personal correspondence), this species is abundant also in the state of Cojedes, Venezuela.

In Colombia (Dugand, 1955) the young leaves are used for making coarse hats, older leaves are utilized in thatching peasants' homes, and the trunks are used as posts. For Venezuela, Pittier (1926) discusses approximately the same general uses. Hershkowitz has written us that the fruits of *C. tectorum* are most important in fattening domestic swine in parts of Colombia where these palms grow; and Jahn (1908) says that, according to Schlim, the natives in the vicinity of Santa Marta eat the fruits also.

EXCLUDED SPECIES

Copernicia campestris Burmeist., Reise La Plata **2**: 48. 1861.

(Type from Córdoba, Argentina, *Lorentz 1261* [B].) = **Trithrinax campestris** (Burmeist.) Drude and Griseb., Symb. Fl. Arg., Goett. Abh. **24**: 283. 1879.

We have not seen the actual type specimen, for it was not among the material examined by us from the Berlin-Dahlem Herbarium. Apparently it was destroyed during World War II. An examination of Beccari's (1931) illustrations (Plate 27, Figs. 1–2), however, shows exserted stamens and no stamen-ring, while the photograph (Plate 34, Fig. 3) shows a type of spathe and spadix not characteristic of *Copernicia*.

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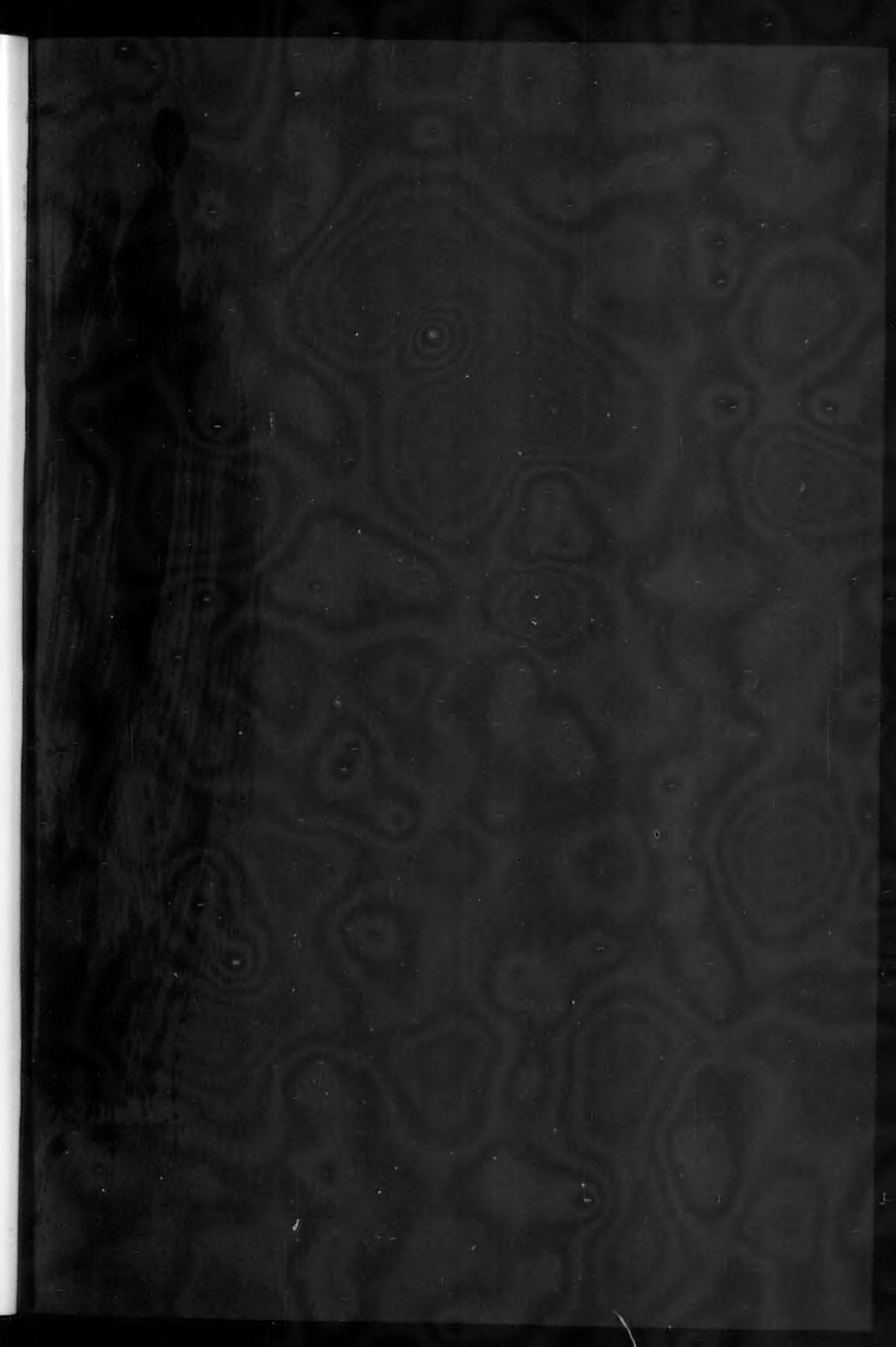
Explanation of Plates in Pocket

PLATE I. South America, showing distribution of *Copernicia* (shaded areas): 1. *C. cerifera;* 2. *C. alba;* 3. *C. tectorum.*

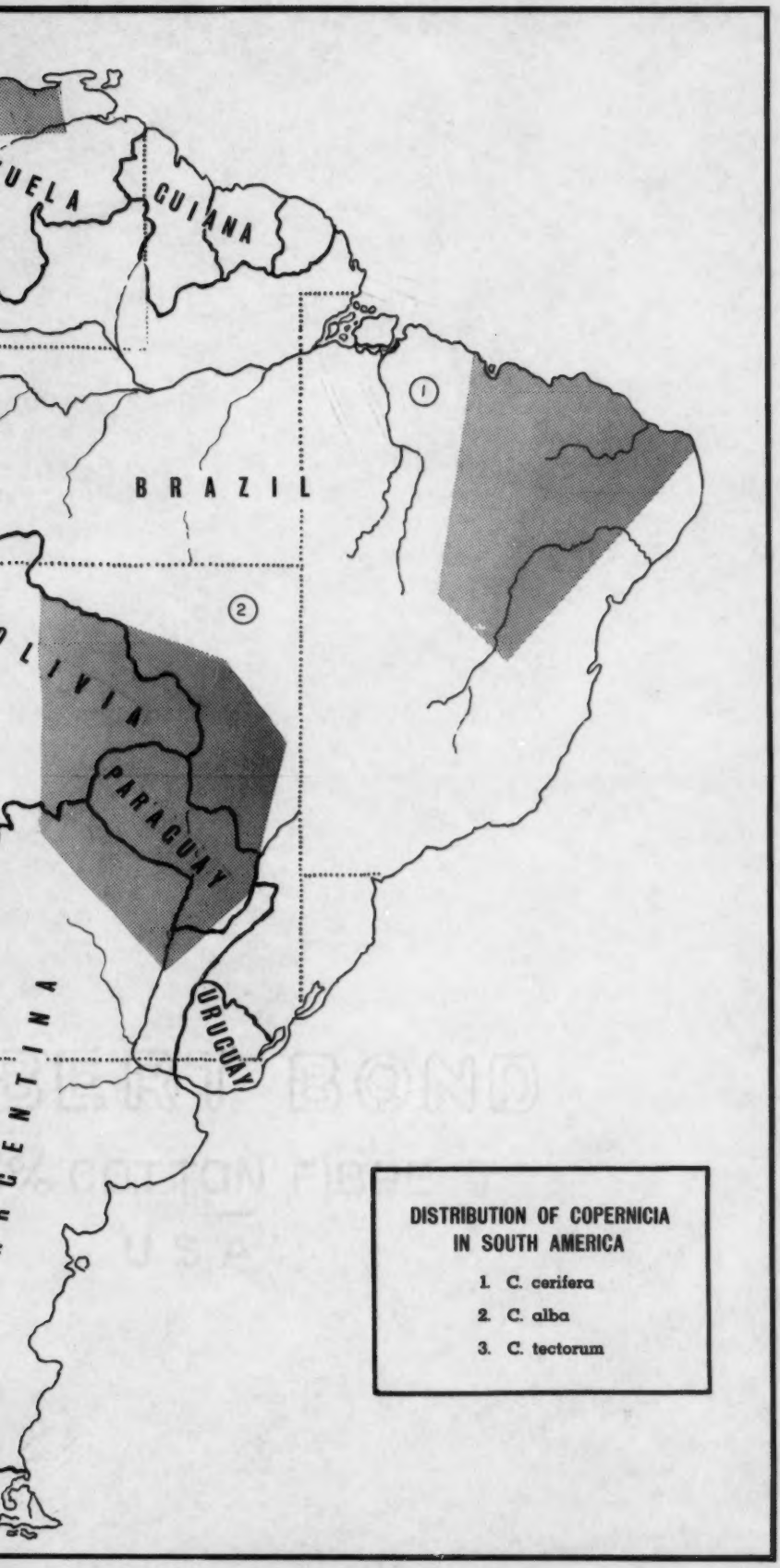
PLATE II. Distribution of *Copernicia cerifera.* Shaded areas are based on map surveys prepared for S. C. Johnson & Son, Inc., by Steinle (unpublished) and a series of maps made by Luetzelburg (1923). Numbers on map refer to localities of actual specimens examined or to localities mentioned in the literature. Number 6 is based on an article and photo by Karsten & Schenck (1908); 7 is from Gardner (1849); 8–10 and 11 and 12 are based on articles by Luetzelburg (1922–23) and Arruda da Camara (1810), respectively; and numbers 13–17 are from Sampaio (1934). All other numbers are based on specimens actually seen by the authors.

PLATE III. Distribution of *Copernicia alba.* Number 1 is based on a specimen cited by Martius (1838); 2–5 are from Martius (1844); 6 and 13 are from specimens cited by both Beccari (1907) and Burret (1928); 10 and 11 are based on articles by Kuntze (1898) and Barbosa Rodrigues (1898); numbers 14–20 are from an article and photos by Lindman (1900); 21, 30, and 31 are based on articles and photos by Parodi (1934) and Frenguelli (1941); and 38 is from Jones (1930). All other numbers are based on specimens seen by the authors.

PLATE IV. Distribution of *Copernicia tectorum.* Numbers 2–8 are from H.B.K. (1816) and 14 and 15 from Hershkowitz (personal correspondence). All other numbers refer to specimens examined by the authors.



3
VENEZUEL
COLOMBIA
ECUADOR
PERU
BOL
CHILE
ARGENTINA



DISTRIBUTION OF COPERNICIA IN SOUTH AMERICA

1. C. cerifera
2. C. alba
3. C. tectorum

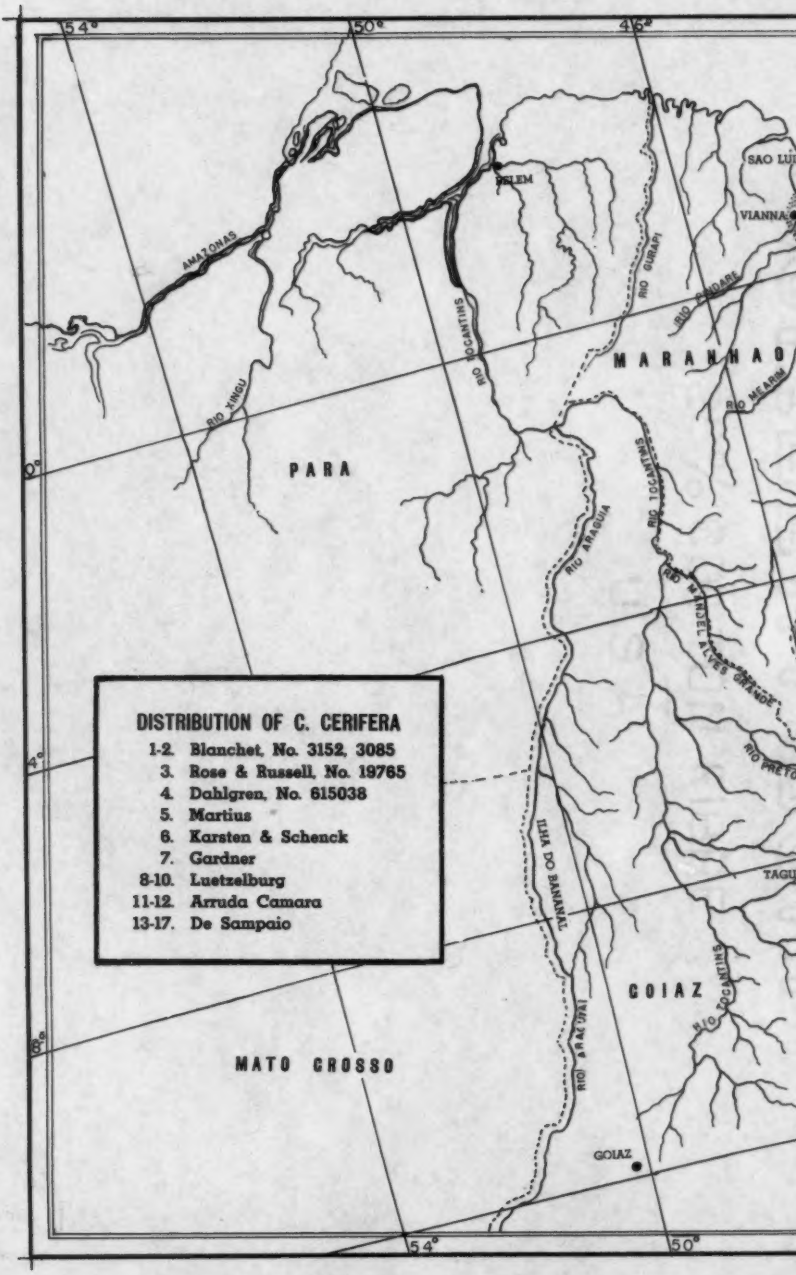
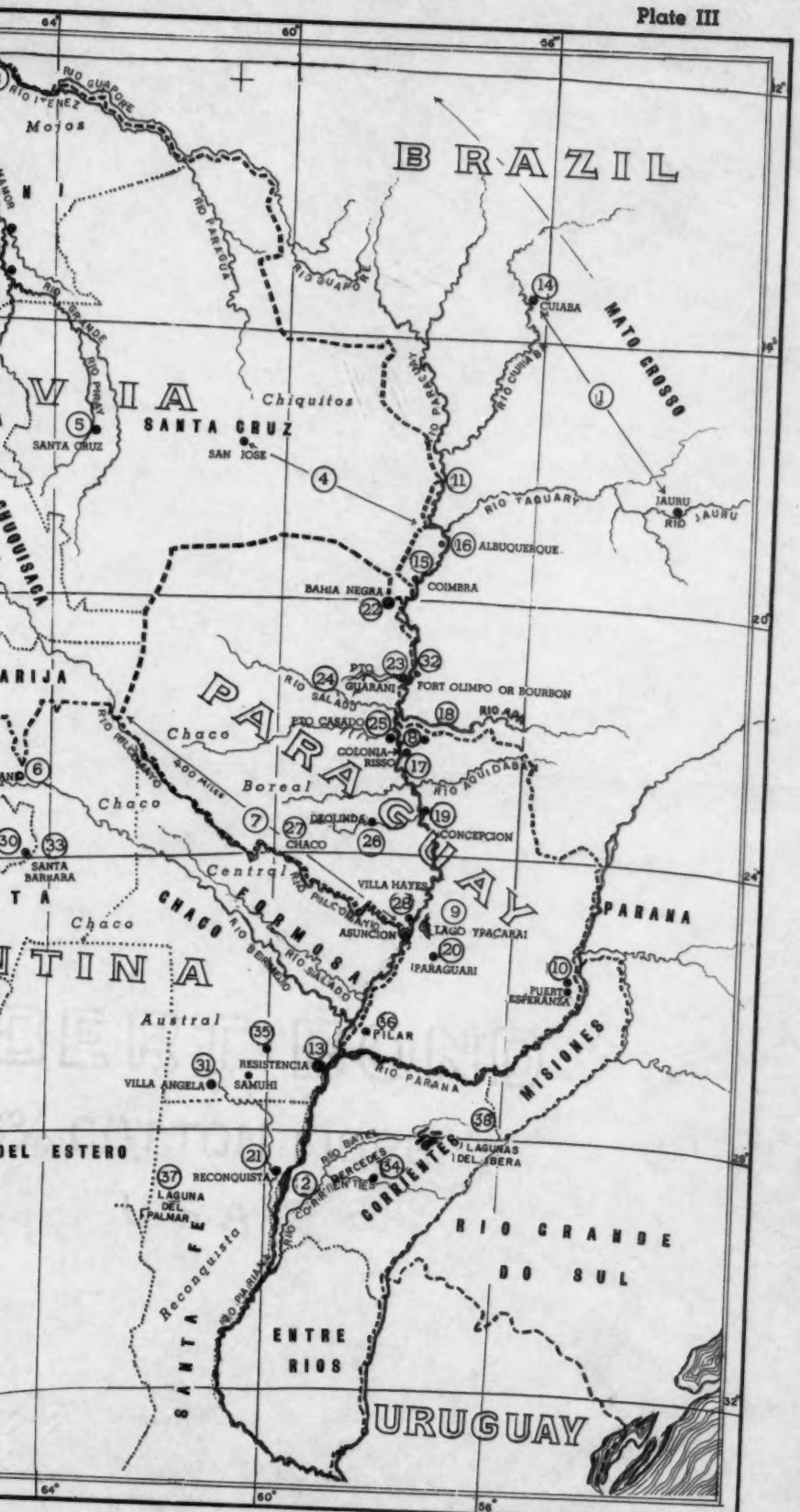

54°
50°
46°
0°
4°
8°
PARA
MARANHAO
MATO GROSSO
GOIAZ
BELEM
SAO LU
VIANNA
AMAZONAS
RIO XINGU
RIO TOCANTINS
RIO GURUPI
RIO PINDARE
RIO MEARIM
RIO ARAGUAIA
ILHA DO BANANAL
RIO ARAGUAIA
RIO TOCANTINS
RIO PRETO
TAGU
GOIAZ
DISTRIBUTION OF C. CERIFERA
1-2. Blanchet, No. 3152, 3085
3. Rose & Russell, No. 19765
4. Dahlgren, No. 615038
5. Martius
6. Karsten & Schenck
7. Gardner
8-10. Luetzelburg
11-12. Arruda Camara
13-17. De Sampaio

Plate II

42°
38°
34°
0°
4°
8°
12°
46°
42°
38°
13 ACARAU
CAMOCIM
PARACURO
FORTALEZA
(CEARA)
4
SAO LUIZ
ARAYOSES
SOBRAL
ARACATI
VIANNA
BREJO
CANINDE
MOSSORO
12
NATAL
AGARAU
RIO GRANDE
DO NORTE
CODO
PIAUHY
APODI
JOAO PESSOA
(PARAIBA)
TERESINA
2
CEARA
PIANCO
PARAHYBA
14
11
RECIFE
AMARANTE
PICOS
JAICOS
PERNAMBUCO
JERUMENHA
URUSSU
PARNAHYBA
BOA VISTA
5
SANTO
ANTONIO
DA GLORIA
15
ALAGOAS
MACEIO
PIAUI
10
ESTROLINA
RIO SAO
FRANCISCO
8
BOM JESUS DA
GURGUEIA
6
REMANSO
CASA NOVA
3
SERGIPE
ARACAJU
9
LAGOA
PARNAGUA
MONTE SANTO
PILAO ARCADO
RIO POCO COMPRIDO
B A I A
FORMOSA
BARRA
RIO PARAGUASSU
PARAGUASSU
SAO SALVADOR (BAIA)
BARREIRAS
16
TAGUATINGA
BOM JESUS
DA LAPA
RIO DAS CONTAS
1
SANTO ANTONIO
RIO CORRENTE
17
CARINHANHA
JACARACI
RIO GAVIAO
SAO FRANCISCO
MINAS GERAIS
PIRAPORA

DISTRIBUTION OF C. ALBA

1. Da Silva Manso
2-5. Martius
6. Lorentz & Hieronymus, No. 582
7. Morong, No. 1073, 1078, 1079
8. Fiebrig, No. 4429
9. Hassler, No. 12393
10. Kuntze
11. Barbosa Rodrigues
12. Werdermann, No. 2227
13. Spegazzini
14-20. Lindman
21. Parodi
22. Markley
23-28. Markley & Kitzke
24. Markley & Kitzke
25. Markley & Kitzke
26. Markley & Kitzke
27. Markley, No. 1-5, 7-8, 10-12
28. Markley, No. 1-3
29. McLoud, No. 405275
30-31. Frenguelli
32. Weddell, No. 3200
33-34. Cabrera, No. 4075, 10537
35-36. Meyer, No. 9857, 16106
37. Ragonese, No. 3033
38. Jones


BRAZIL
PARAGUAY
Chiquitos
Chaco
Boreal
Central
Austral
Chaco
SANTA CRUZ
SAN JOSE
SANTA CRUZ
CUIABA
MATO GROSSO
JAURU
RIO JAURU
RIO TAQUARY
ALBUQUERQUE
COIMBRA
BAHIA NEGRA
PTO GUARANI
FORT OLIMPO OR BOURBON
PTO CASADO
COLONIA RISSO
RIO AGUIDABAN
DEOLINDA
CHACO
CONCEPCION
VILLA HAYES
ASUNCION
LAGO YPACARAI
IPARAGUARI
PUERTO ESPERANZA
PARANA
MISIONES
PILAR
RESISTENCIA
SAMUHU
VILLA ANGELA
RIO PARANA
LAGUNAS DEL IBERA
CORRIENTES
RECONQUISTA
LAGUNA DEL PALMAR
RIO GRANDE DO SUL
ENTRE RIOS
URUGUAY
SANTA FE
Reconquista
RIO PARANA
RIO CORRIENTES
RIO BATEL
RIO SALADO
RIO PILCOMAYO
RIO BERMEJO
RIO GUAPORE
RIO IYNEZ
RIO PARAGUA
RIO GUAPAY
RIO PILCOMAYO
RIO PARAPETI
RIO CUIABA
RIO GRANDE
RIO PIRAY
400 Miles
64°
60°
56°
12°
16°
20°
24°
28°
32°

80°
76°
72°
12°
8°
4°
0°
18
SANTA MARTA
BARANQUILLA
19
ATLANTICO
CIENAGA DE GUAJARO
CIENAGA
De Santa Marta
14
16
17
15
MAGDALENA
GUAJIRA
ZULIA
LAGO DE MARACAIBO
TRUJILL
MERIDA
BA
BOLIVAR
RIO SINU
RIO SAN JORGE
RIO CAUCA
RIO MAGDALENA
N. DE SANTANDER
TACHIRA
ANTIOQUIA
SANTANDER
ARAGUA
CHOCO
CALDAS
CUNDINAMARCA
BOYACA
RIO META
VALLE
CAUCA
TOLIMA
COLOMI
META
CAUCA
HUILA
VAUPE
NARINO
CAQUETA
PUTUMAYO
ECUADOR
AMAZONAS
PERU

Plate IV

DISTRIBUTION OF C. TECTORUM

1. Bonpland, No. 796
2-8. H. B. K.
9. Tamayo, No. 3504
10. Woronov, No. 7275
11. Pittier, No. 11302
12. L. Williams, No. 13275
13. Brother Gines
14-15. Hershkowitz
16. Schlim, No. 954
17. Foster & Smith, No. 1628
18. Bailey, No. 240, 254
19. Dugand, No. 299